NEW ZEALAND SPECIES OF THE PERMIAN BIVALVE *ATOMODESMA* BEYRICH

by J. B. WATERHOUSE

ABSTRACT. Eight species of *Atomodesma* are described from New Zealand, ranging from basal to topmost Permian. The following new species are described: *A. obliquatum*, *A. woodi*, and *A. trabeculum*.

THE genus *Atomodesma* Beyrich is the most abundant and widespread fossil known from the New Zealand Permian. It occurs at almost every fossil locality in the Permian of the marginal and shelf facies of the Southland and Nelson synclines, and fragments of its shell are scattered throughout the otherwise barren greywackes of Canterbury and north Otago. Much of the widespread Wooded Peak and correlative limestones seems to be made up of *Atomodesma* prisms, and lenses of limestone at the base of the Stephens Formation are of a similar composition.

Only two species have been named hitherto: *Atomodesma trechmanni* (Marwick 1934) and *A. marwicki* Waterhouse 1958. A fragment was also described by the writer in a note included in a paper by Bruce (1962). A further six species are recorded, and three named in the present work. Most of the Lower Permian species are found in western Southland in the Takitimu Mountains and foothills, and the Upper Permian species are found in Nelson, north-west Southland, and south Otago (text-fig. 1, table 1). The fossil localities are described in an appendix: each locality is numbered serially with the prefix GS.

As mentioned in the text, some specimens are kept at the British Museum (Natural History), and some at Otago University, Dunedin. The remaining specimens are stored at the New Zealand Geological Survey, Lower Hutt, and are registered serially by numbers with the prefix TM.

SYSTEMATIC PALAEONTOLOGY

Genus ATOMODESMA Beyrich 1864

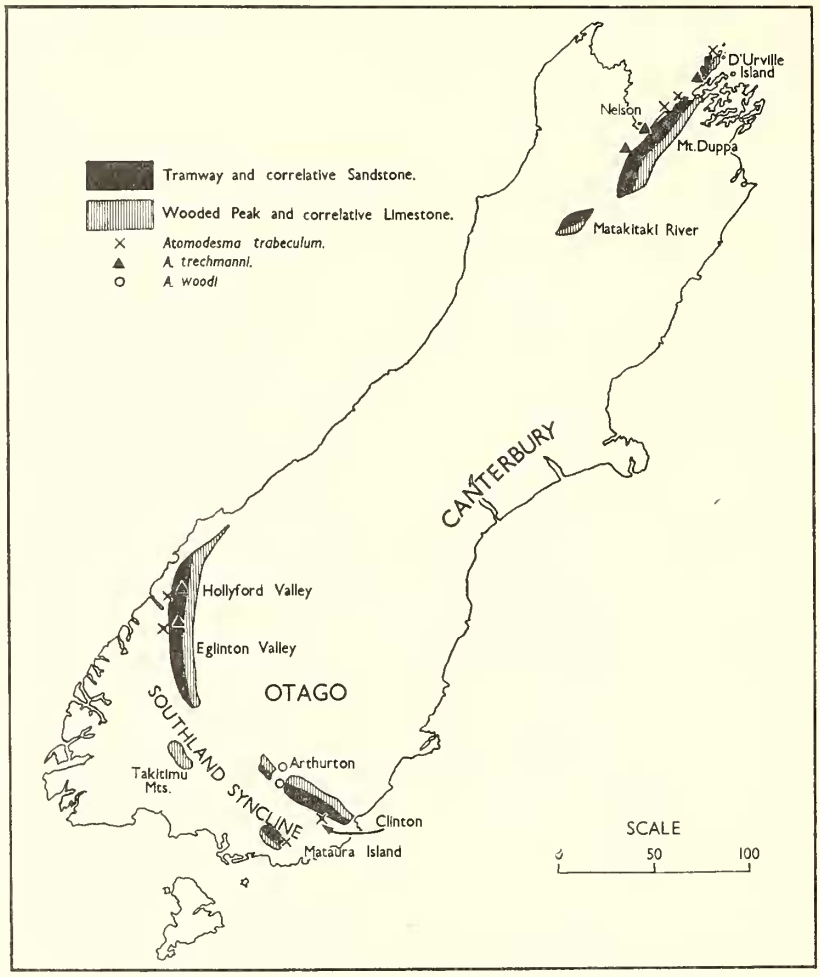
Type species. Atomodesma exaratum Beyrich, subsequently designated by Wanner 1922, p. 63.

Diagnosis. Large biconvex shells, with anterior prosogyrous or orthogyrous beaks, a weak byssal gape in many species, a small anterior ear in some, and generally a large posterior wing. Ornament of low concentric wrinkles, with or without radial plicae. Ligament area largely or entirely posterior, edentulous, striated by growth-lines. An umbonal septum present in both valves (text-fig. 2). Anterior adductor scar uncertain. Posterior adductor scar large, pallial line integripalliate, pitted. Shell prismatic. Permian of Africa, Salt Range, Karakorum, Russia, Australia, Indonesia, New Caledonia, and New Zealand.

Discussion. (*a*) *Subgenera.* Several genera have been erected for forms that were not

[Palaeontology, Vol. 6, Part 4, 1963, pp. 699–717, pl. 100–5.]

originally recognized as being closely allied to, or congeneric with, *Atomodesma exaratum*. These include *Aphanaia* de Koninck 1877, from Australia, and *Maitaia* Marwick 1934, from New Zealand. In 1956 Dickins showed that *Aphanaia* is probably congeneric with



TEXT-FIG. 1. Distribution of the Kazanian Wooded Peak Limestone and Tramway Sandstone of the Nelson Syncline and correlative beds of the Southland Syncline, with *Atomodesma* species. The width of the rock belts is exaggerated.

Atomodesma, and in 1958 the writer synonymized *Maitaia* with *Atomodesma*. The Russian workers B. K. Likharev and U. N. Popov, on the other hand, subdivided *Atomodesma*, erecting the genera *Kolymia* Likharev 1941 (see Likharev and Einor 1941), and *Intomodesma* Popov 1958. Dickins (1961*a*, p. 123) and the writer (1959) preferred to emphasize the closeness of these forms to *Atomodesma exaratum*, and proposed that the genera be relegated to subgenera. *Atomodesma* (*Atomodesma*) has radial plicae, *Kolymia* Likharev has anterior ears and is not plicate, and *Aphanaia* de Koninck is said to be inequivalve and lacks plicae or anterior ears. *Maitaia* Marwick and *Intomodesma* Popov are

close to *Aphanaia* in that they lack anterior ears and are not plicate. Although they appear to be equivalve, they were tentatively regarded as synonymous with *Aphanaia*. The writer now considers that plication is not of generic or even subgeneric significance. The anterior ear of *Kolymia* is probably an important feature and forms, with the rest of

TABLE I. Occurrence of New Zealand species of *Atomodesma*

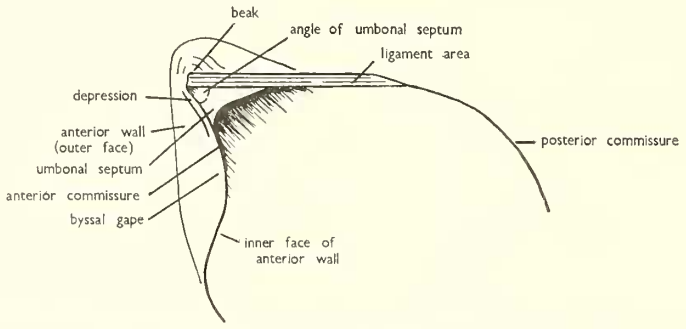
Russian Standard	SOUTH ISLAND NEW ZEALAND					
	Southland Syncline				Nelson Syncline	
	Western Southland SW limb	South Otago NE limb	Mataura Island S limb	Hollyford, Eglinton Valleys N limb	E limb	W limb
Tartarian	Productus Creek Group: Wairaki Breccia	Arthurton Group		Bayneira Group: Countess Formation	Maitai Group: Stephens Formation *Atomodesma* B	
Kazanian	Productus Creek Group	Arthurton Group: *A. trabeculum*	Kuriwao Group: Titiroa Limestone *A. trabeculum* Pine Bush Formation	Bayneira Group: Winton Formation; Tapara Formation; *A. trabeculum* Annear Formation *A. trechmanni*	Maitai Group: Waiua Formation; Greville Formation; *A. trabeculum* Tramway Formation *A. trechmanni*	
	Productus Creek Group: Elsdun Limestone	Arthurton Group: AG4 Limestone *A. woodi*	Kuriwao Group: Waimahaka Limestone	Bayneira Group: Howden Limestone	Maitai Group: Wooded Peak Limestone	
Kungurian	Productus Creek Group: Mangarewa Formation *A.* aff. *mitchelli*					
Artinskian	Productus Creek Group: Letham Formation *A. obliquatum*			Humboldt Group	Lee River Group	*Atomodesma sp.* Brook Street Volcanics
	Takitimu Group	*A. marwicki* Waipahi Group				
Sakmarian	*Atomodesma* sp. A.					

the umbonal region, the crucial part of the shell. But the umbonal region has scarcely ever been figured or described in detail in Russian and Australian shells. As a result the type species of *Kolymia*, *Intomodesma*, and *Aphanaia* are so inadequately known that the writer proposes to refer all these related taxa to *Atomodesma*, at least until the vital structures are fully described.

The umbonal region varies in different New Zealand species, and is consistent within each species. In several species the ligament area ends just in front of the beak, the umbonal septum is below the area, and is bounded in front by the anterior wall of the shell, which is in these forms normal to the commissure. This part is slightly but sharply depressed below the rest of the anterior face of the shell (the 'depression' in text-fig. 2). The depression is related to a narrow byssal gape, and passes upwards towards the ligament area. Such an arrangement is seen in New Zealand species from the Letham

Formation, from the widespread Upper Permian Wooded Peak limestone, and in the specimen of *A. variabilis* figured by Wanner (1940, text-fig. 1, p. 9), of which a mould was kindly sent to the writer by Prof. MacGillavry from the Geological Instituut of Amsterdam. The depression is feebly developed also in a species from the upper Tramway Sandstone of New Zealand.

Several species from New Zealand have a small anterior ear. This ear is of different structure in different species. In one from the Upper Permian Stephens Formation, Nelson, the parts of the anterior walls which lie between the umbonal septa and commissure of the two valves are inclined forward, instead of lying normal to the commissure. The



TEXT-FIG. 2. Dorsal anterior part of a right valve of *Atomodesma*, showing the ligament plate and umbonal septum.

depressed area next to the commissure is well defined in this species, as in *A. variabilis*. In the oldest *Atomodesma* from New Zealand, the anterior walls between the septa lie flush with the tops of the septa and are scarcely depressed below the rest of the shell. In *A. marwicki* Waterhouse the entire septum lies in front of the beak, judging from an internal mould, and the anterior wall next to the septum does not seem to be depressed. Here then are three kinds of anterior 'ear', and it is not certain that the three species are more closely related to one another than to forms without ears.

Yet another arrangement is present. *A. trechmanni* (Marwick) has no ear, and the depressed region in front of the ligament curves laterally well away from the commissure.

(*b*) *Characters of specific importance.* The umbonal region is of foremost importance in circumscribing the specific characteristics of the New Zealand *Atomodesma*. The shape of the umbonal septum and the angle of the septum (measured between its anterior and dorsal edges, i.e. the inner edge of the anterior wall, and the inner edge of the hinge), the nature of the anterior margin immediately in front of the septum, and the anterior end of the ligament area, are consistent within each species and differ considerably from species to species. The definition of the posterior wing, the height and curvature of the umbo, and the shape of the shell, are of secondary importance, tending to vary laterally at the same horizon. The strength of the concentric wrinkles varies even more, as does the diameter of prisms in the shell. The striations of the ligament area and the muscle scars do not appear to differ significantly from species to species.

(*c*) *Structure of the shell.* The shell structure comprises hexagonal or polygonal prisms normal to the shell surface, ranging in diameter from 0·025 to 0·05 mm., and of the same

diameter on each valve. Under crossed nicols the prisms extinguish for their complete length, although interrupted by weak and strong growth-lines. In a few specimens the prisms taper towards a strong growth junction, and a few interstitial trigonal prisms appear. But as a rule the prisms are parallel-sided.

In 1958 the writer reported that a fibrous outer layer was present on a fragment from GS 6323. When forwarded to be sectioned, it shattered and the shell was destroyed. As a result the structure has not been verified, and the writer is inclined to consider that the layer may have been recrystallized, or composed of fine prisms, for no fibrous or lamellar structure has been seen in other sections.

The shell where a muscle scar is situated was sectioned; no hypostracum is visible; the structure remains prismatic. However, Wanner (1922, p. 61, text-fig. 12) recorded a thin inner layer in *A. exaratum*.

Inoceramus, another prismatic shell common in New Zealand, has much thicker prisms, and its inner non-prismatic layer is frequently preserved.

Atomodesma sp. A

Plate 100, figs. 1, 3

Maitaia sp. Mutch 1957, p. 501.
Atomodesma sp. nov. Waterhouse 1958*b*, p. 605.

Material. Two specimens are available, one a fragmentary internal mould, the other an external mould, both of the beak region. Other fragments and prisms are also present.

Diagnosis. Beak weakly prosogyrous, ligament area almost completely open at anterior end. anterior part of septum apparently lying within a small anterior ear.

Horizon and locality. Takitimu Group, Permian; GS 5885.

Dimensions (in mm.). A right valve, from a growth-line.

Specimen	*Length*	*Height*	*Width*	*Umbonal angle*
TM 3786	17·5	19·5	6	75°

Description. External. The specimens are so fragmentary that only a few details can be described. The beak is very weakly prosogyrous, and the anterior face is steep and incurved. The shell is smooth apart from very low growth wrinkles.

Internal. The ligamental area is concave under the beak, and flatly concave posteriorly, and is weakly striated by longitudinal growth-lines and weak vertical lines. The area does not extend in front of the beak, and is almost completely open at its anterior end except for a very short ridge above the umbonal septum. Between the ligament and the anterior commissure is a concave umbonal septum, with the angle between its anterior and dorsal margins measuring about 50°. The anterior part of the septum seems to lie at the level of the commissure and to extend beyond the beak within a small ear, although this is possibly due to crushing. A narrow groove is present on the outer surface, parallel to and placed 1 mm. from the commissure.

Shell structure. Prisms are long and about 0·03 mm. in diameter.

Affinities. Maitaia trechmanni Marwick 1935, pl. 34, figs. 1–3, from the Upper Permian Tramway beds of Nelson, has a wider umbonal angle (70°), stronger concentric growth

wrinkles, and no anterior ear. The ligament area beneath the beak of *trechmanni* is more constricted by the umbonal septum, and the septum is set well below the commissure.

The umbonal fragment of *Atomodesma* recorded by Waterhouse (*in* Bruce 1962, p. 166) from the Brook Street Volcanics is like the Takitimu form in its beak and anterior end of the ligament area, but apparently lacks an anterior ear, and has a septum set well below the commissure.

Atomodesma marwicki Waterhouse 1958

Plate 100, figs. 2, 4

Maitaia sp. Marwick *in* Wood 1956, p. 38, fig. 18.
Atomodesma marwicki Waterhouse 1958*a*, p. 173, fig. 2*a*.
Atomodesma (*Kolymia*) *marwicki* Waterhouse 1959, p. 260.

Material. More specimens have been collected from the type locality of *marwicki*, but add little to the description of the species.

Horizon and locality. Waipahi Group, Permian; GS 5082.

Holotype. TM 2035.

Diagnosis. Septum placed anterior to the beak, and largely anterior to the inner face of the anterior wall.

Description. The species is described by Waterhouse (1958*a*).

Atomodesma obliquatum sp. nov.

Plate 100, figs. 5–7

Material. A large left valve, a crushed specimen with valves conjoined, an umbonal fragment, and two small left valves. Specimens etched in acid to show internal details. It is not known whether the shells are equivalve or not.

Horizon and locality. Productus Creek Group, Letham Formation, Permian; GS 7344.

Holotype. TM 3366 (Pl. 100, fig. 5). *Paratypes.* TM 3365, 3426, 3427.

Diagnosis. Oblique shell, posterior wing small, ligament constricted by a ridge which passes upward from the anterior end of the umbonal septum, septum thin and plate-like, and the adjoining anterior wall between the septum and anterior commissure is depressed below the rest of the outer face of the anterior wall.

Dimensions (in mm.). (left valves)

Specimen	*Length*	*Height*	*Width*	*Hinge length*	*Umbonal angle*	*Angles a*	*b*	*c*
TM 3426	30	38	? 11	19	85°	55°	40°	90°
TM 3366	90	100	21	27	60°	50°	40°	85°

EXPLANATION OF PLATE 100

Figs. 1–3. *Atomodesma sp.* A. PVC cast of umbonal region, TM 3364, GS 5885, ×2.
Figs. 2, 4. *Atomodesma marwicki* Waterhouse. 2, Rubber latex cast of umbonal region. 4, Internal mould of holotype TM 2035, GS 5082, ×1.
Figs. 5–7. *Atomodesma obliquatum* sp. nov. 5, Internal mould of holotype, left valve TM 3366. 6, Internal mould and hinge of paratype TM 3426. 7, Rubber latex cast of umbonal region of TM 3427; the lower right outline of the figure defines the lower edge of the umbonal septum; GS 7344, ×1.
Figs. 8–10. *Atomodesma sp.* aff. *A. mitchelli* M'Coy. 8, PVC cast of crushed right valve TM 3537, GS 6072. 9, PVC cast of TM 3535, GS 6072. 10, External rubber latex cast of TM 3540, GS 7350. ×1.

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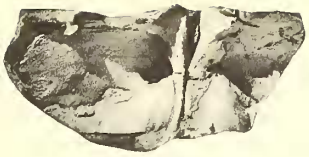

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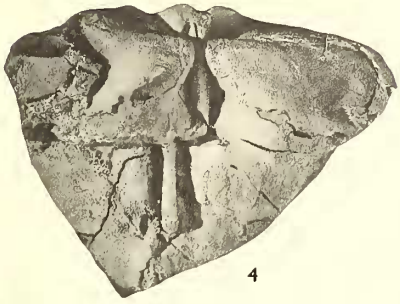

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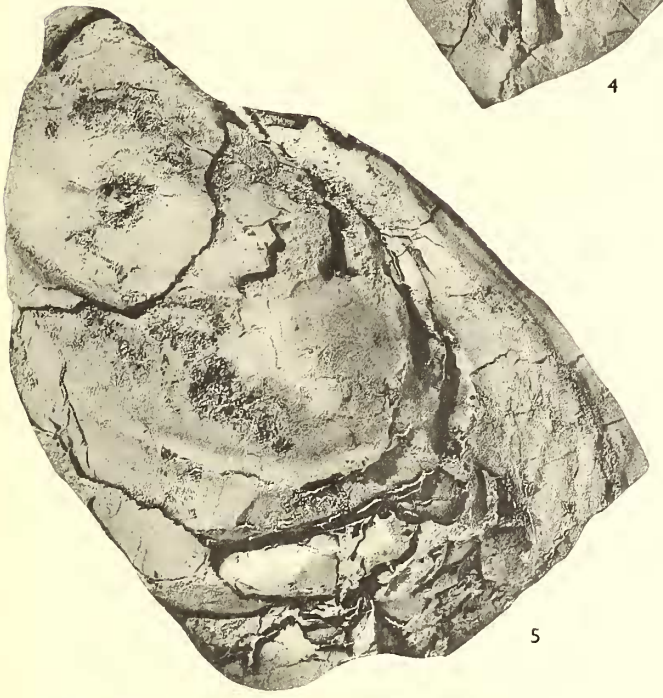

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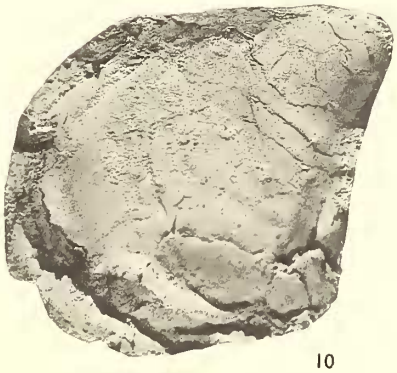

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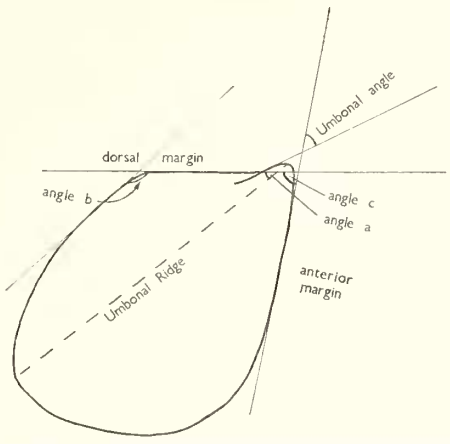
WATERHOUSE, *Atomodesma*

Description. External. These are the best-preserved specimens of *Atomodesma* from the Lower Permian of New Zealand. The valves are prosocline, with an anterior weakly prosogyrous umbo, steep anterior wall, and a short hinge. Between the septum and commissure the anterior wall is depressed like a flange. A small posterior wing is developed, with a narrow angle of only 25°. Irregular concentric wrinkles cover the shell.

Internal. The ligament area is concave and striated, with longitudinal ridges in the larger specimens but not in the small TM 3426. The area is thickened moderately, and is constricted at the anterior margin by a low ridge that extends from the dorsal anterior end of the umbonal septum. The umbonal septum is thin and plate-like, with an angle close to 50°, and has a curved dorsal margin. The underside of the septum and the ligament form one continuous surface. In the small specimen TM 3426 the septum is very small.

The posterior adductor muscle scar is visible in TM 3366. It lies close to mid-height, below the posterior end of the hinge, and is bean-shaped, with a small lobe adjoining a large ventral lobe. No pallial line or anterior scar is visible.

Shell structure. Prisms are 0·05 mm. in diameter, and the shell as a whole is normally 0·8 to 1 mm. thick.



TEXT-FIG. 3. Right valve of *Atomodesma*, showing how the angles are measured. The umbonal angle is measured between the anterior and dorsal margins of the first formed part of the shell. Angle *a* is measured between the dorsal margin of the shell behind the umbo and the umbonal ridge (as in Newell 1942, p. 22). Angle *b* is measured between the dorsal margin and the dorsal part of the posterior margin (Newell 1942). Angle *c* is measured between the dorsal margin and the anterior margin.

Affinities. This species has more concentric wrinkles and a narrower posterior wing than in the Takitimu *Atomodesma*. The part of the anterior wall between the septum and commissure is depressed and normal to the commissure, whereas it is apparently almost continuous with the rest of the exterior and points forward like an ear in the Takitimu specimen. Also the ligament of *A. obliquatum* is more constricted under the umbo.

A. trechmanni (Marwick) from the Upper Permian of New Zealand has a larger posterior wing, a produced rather than depressed anterior commissure, with subterminal beaks, and a larger, more bulbous ridge protruding above the umbonal septum into the ligament area.

Inoceramus mitchelli M'Coy 1847 from Eastern Australia has similar ornament and a similar narrow posterior wing, but is less oblique and has a longer hinge.

Perhaps the closest specimens are those figured as *A.* cf. *timorense* Wanner by Dickins (1963, pl. 9, figs. 8, 10–12) from the Artinskian Callytharra Formation and Nura Nura Member of Western Australia. The Australian shells have a high tumid beak and prominent posterior wing, as in Wanner's specimens from the Artinskian beds of Niloelet, Timor. Unfortunately the details of the umbonal region of *timorense* are not available for comparison. *A. timorense* has a higher beak and greater inflation than the associated

species *A. mytiloides* Beyrich 1864, from the Bitauni beds of Timor, and the Callytharra Formation, Poole Sandstone, Fossil Cliff Formation, Noonkanbah Formation, and Byro Formation of Western Australia, but the umbonal structures must first be known in order to determine the significance of these differences: they may be only subspecific or varietal.

Atomodesma sp. aff. *A. mitchelli* M'Coy 1847

Plate 100, figs. 8–10; Plate 101, fig. 1; Plate 105, figs. 8, 9

Material. Two right valves and a left valve showing the hinge, a damaged specimen with valves conjoined, and large and small fragments from GS 6072. Natural external moulds of two right valves from GS 7350 and fragments from GS 3616 come from the same formation and so might be conspecific. All specimens incomplete and crushed.

Horizon and localities. Mangarewa Formation, Permian; GS 6072, ? 3616, ? 7350.

Diagnosis. Small well-rounded shell with terminal weakly prosogyrous beak and a very narrow posterior wing, concentric wrinkles usually well developed.

Dimensions (in mm.), estimated from broken specimens. GS 6072.

Specimen	*Length*	*Height*	*Width*	*Hinge length*	*Umbonal angle*	*Angles a*	*b*	*c*
				Right valve				
TM 3535	45	40	15	31	80°	45–50°	30°	105°
				Left valve				
TM 3536	45	38	? 13	27	—	45°	50°	90°

Description. External. The shells are small and moderately inflated, with a subquadrate outline, and weakly prosogyrous terminal beaks. The anterior wall is unusually wide. It is flattened on the beak, and below the hinge lies normal to the commissure. In each specimen a furrow 2 or 3 mm. wide arises at the commissure just below the umbonal septum, and passes dorsally almost to the anterior end of the ligament. The furrow might be due to crushing but looks like a byssal groove, marked as it is by several wrinkles.

Only a very narrow posterior wing is present. Apart from the first formed part of the shell, which is almost smooth, the specimens from GS 6072 have strong concentric growth rugae which are occasionally overturned on the ventral side. One to three lower concentric wrinkles lie on each prominent ruga. The two valves from GS 7350 have only low wrinkles.

Internal. The face of the ligament area is inclined in section at 20° to 30° dorsally away from the commissure. The area is not supported by heavy thickening. Under the beak it is strongly concave and is constricted by a low convexity which lies above the

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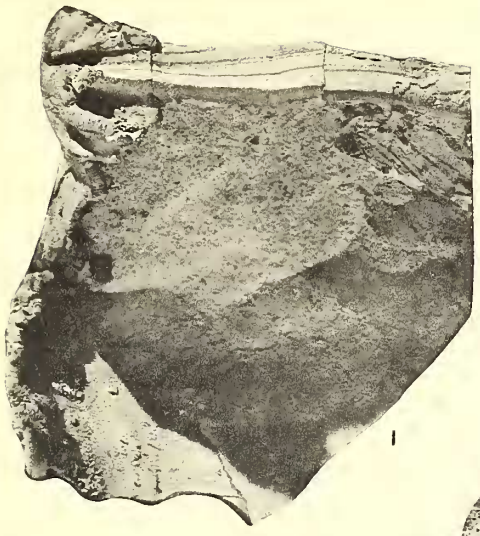
EXPLANATION OF PLATE 101

Fig. 1. *Atomodesma sp.* aff. *A. mitchelli* M'Coy. Part of PVC cast of umbonal region, TM 3535, GS 6072, ×2.

Figs. 2–5. *Atomodesma woodi* sp. nov. 2, Rubber cast showing long umbonal septum, OU 2436, GS 4652, ×1. 3, Internal mould of right valve TM 2037 from GS 4586, showing posterior muscle scar, ×1. 4, Holotype, PVC cast, TM 3645, GS 4652, ×1. 5, Rubber latex cast of umbonal region with the valves conjoined and opened out to show the umbonal septa separated by the ligament area, TM 3643, GS 4652, ×2.



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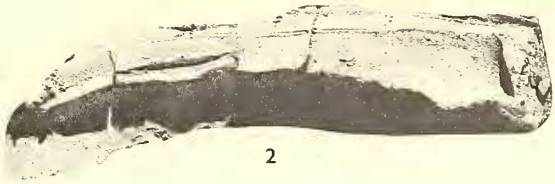

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WATERHOUSE, *Atomodesma*

umbonal septum; posteriorly it widens and becomes flatter. About three longitudinal grooves, separated by sharp ridges, are present on the area, the dorsal grooves passing back on to the body of the shell and the inner one commencing at the convexity. The area is also marked by fine longitudinal ridges (3 or 4 in 1 mm.) and by even finer vertical striae, corresponding with the prismatic structure of the shell.

The umbonal septum is set 2 mm. below the commissure, and is prolonged posteriorly for half the length of the hinge as a narrow ledge. In TM 3537 it is acutely angular at the apex under the beak, with an angle of 45° between its anterior and dorsal margins. In the other two specimens, TM 3535 and 3536, the apex is rounded, and the angle of the septum as a whole is only 30° or 40°.

Muscle scars and pallial line are uncertain.

Shell structure. The shell away from the umbonal region is up to 1·5 mm. thick. Thin sections show that the prisms are usually 0·025 mm. in diameter in specimens from both GS 6072 and 3616. In some specimens from GS 3616 the prisms are 0·05 mm. in diameter. The prisms are usually hexagonal, or almost so, in cross-section, but are sometimes square.

Affinities. The Mangarewa shells lack the anterior ear of the Takitimu *Atomodesma sp.* A, and also have a more constricted ligament area under the beak, and slightly more prosogyrous beaks.

The Letham species *A. obliquatum* sp. nov. is more oblique and has a better defined posterior wing, and a more thickened ligament area. The anterior wall of *A. obliquatum* is depressed close to the commissure to form a narrow flange, and lacks any signs of a broad byssal groove.

A. trechmanni (Marwick) has a much larger posterior wing and is a larger, less inflated shell, with subterminal beaks. The umbonal septum and anterior wall are moderately similar, but the anterior wall of *trechmanni* bulges forward, and the ligament area is thickened more posteriorly and is less inclined from the commissure.

Closest species in shape is *Inoceramus nitchelli* M'Coy 1847 from beds of approximately the same age at Glendon and Wollongong, New South Wales. Plaster duplicates of the holotype and two paratypes have been kindly sent to the writer from the Sedgwick Museum by Mr. A. G. Brighton, and other specimens have been kindly loaned from the Australian Museum by Mr. H. O. Fletcher. The specimens vary in shape and ornament. Closest to the New Zealand specimens are the holotype, and M'Coy's paratype E 10733. These are subquadrate in outline with a wide anterior wall. Strong rugae and a very narrow posterior wing occur in the holotype, as in the New Zealand specimens. The second paratype, E 10732, is a higher shell, with slightly more regular wrinkles, but is otherwise close.

The specimens sent to the writer from the Australian Museum have wide anterior walls but vary a little in shape and ornament. Internal details are preserved in specimen F 48885, figured by Dickins 1963, pl. 9, figs. 14, 15. The ligament area is narrow and concave, as in the small shell TM 3540 from GS 7350, and the umbonal septum is small, and a little thicker than in the New Zealand forms. A septum is also visible in F 2170, figured by Dickins 1963, pl. 9, figs. 16, 17. (Dickins suggested that an anterior ear is possibly present, but this is very doubtful.) In F 48885 the inner side of the anterior wall below the septum bulges inwards where the supposed byssal groove is situated in the New

Zealand specimens. Unfortunately the external mould is not available, so that further details, necessary to establish or disprove the identity of the Australian and New Zealand shells, are not available: similarity in shape and ornament might prove to be misleading.

Atomodesma woodi sp. nov.

Plate 101, figs. 2–5; Plate 102, figs. 1, 4; Plate 105, fig. 12

Maitaia trechmanni, *non* Marwick, Wood 1956, p. 44, figs. 23A, D.

Material. A right valve, two left valves, and three specimens with valves conjoined from GS 4652, four right valves, two left valves, and a specimen with valves conjoined from GS 4586. A left valve from GS 4562 is kept at Otago University. Best preserved of New Zealand *Atomodesma*, showing muscle scars and colour bands as well as other details. About thirty single valves from GS 5077 might be conspecific but do not show the hinge.

Horizon and localities. AG 4 Limestone, Arthurton Group, Permian; GS 4652, 4586, ? 5077.

Holotype. TM 3645, GS 4652 (Pl. 101, fig. 4). *Paratypes.* TM 3641–4, 3646, OU 2436, GS 4652; TM 2037, 3636–40, GS 4586.

Name. After Mr. B. L. Wood, N.Z. Geological Survey, Dunedin.

Diagnosis. Large shell with tiny anterior ear in small specimens, posterior wing usually scarcely defined and wrinkles usually very low. Umbonal septum large, with a wide angle of 80° to 90°; anterior edge of septum almost straight.

Dimensions (in mm.).

Specimen			*Width*		*Hinge*	*Umbonal*		*Angle*	
TM	*Length*	*Height*	*L. valve*	*R. valve*	*length*	*angle*	*a*	*b*	*c*
GS 4586									
3638	59	59	—	8	33	70°	48°	40°	80°
2037	85	?85	?13	—	—	70°	60°	20°	100°
3637	100	88	—	11·5	—	85°	50°	40°	90°
3639	103	96	11	—	—	80°	50°	30°	100°
GS 4652									
3644 *gr*	35	40	4·5	—	—	90°	55°	40°	110°
3645	115	110	—	16	50	70°	50°	20°	85°
GS 5077									
3674 *gr*	11·5	9·5	4	—	8	55°	50°	55°	65°
3675	12·5	12	4·5	—	9	60°	50°	45°	75°
3671	17	22	8	—	11	60°	50°	40°	80°
3672	17	24	—	5·5	12	65°	50°	55°	70°
3676	18	17·5	6	—	?12	60°	45°	40°	—
3673	20	24	10	—	9·5	50°	45°	50°	80°

gr—measured from growth-line.

Description. External. The shells are little inflated, probably equivalve, and large, the biggest specimen TM 3646 measuring more than 12 cm. in length. The beak is terminal, and weakly prosogyrous. Maximum height lies close to the anterior margin of the shell, which is gently convex in outline. A very low anterior ear or ledge projects forward for 1 or 2 mm. from the commissure in front of the umbonal septum in specimens up to 80 mm. long. Adjoining the ledge is a sharp depression, which continues from the anterior end of the ligament. As the shells increase in size, additional layers of shell increase the

width of the ledge, but do not project beyond the first layers, so that the ear-like effect is lost. A posterior wing is usually not developed.

The specimens vary in shape. Some, such as TM 3637, are very high; others, such as TM 2037, are more elongated, becoming so after early ontogeny. Some of the shells are smooth, and others have low, well-spaced concentric wrinkles.

Internal. The ligament area is supported on a sturdy shelf, which is not greatly thickened. It is concave under the beak and lies roughly in the plane of the commissure until beyond mid-length and then turns outward through 90°. Striations and grooves occur as in other species and persist anteriorly beyond the ligament on to the depressed part of the anterior face. The ligament area is not constricted under the beak by the top of the umbonal septum, recalling the areas of the Takitimu and Brook Street specimens. The septum is very large and thin, with its anterior margin straight rather than curved. The angle of the septum varies, measuring 95° in TM 3644, 90° in TM 3643, and about 70° in TM 3638 and 3645. It extends well back from the umbo, particularly in the specimen at Otago University.

The posterior adductor muscle scar is well defined, bean-shaped in outline, placed well below and behind the posterior extremity of the hinge, and marked by low growth lines. A pitted pallial line extends forward from the scar. Nearer the beak a second scar of similar outline is visible in TM 2037 and 3637 from GS 4586, and another pitted line can be discerned in TM 3637, possibly representing gill suspensories.

Shell structure. Radial colour bands of light and dark shell are visible on decorticated specimens from GS 4652 and 4586. The dark bands coincide with the pallial muscle scars, at least in TM 3644.

A thin section of a specimen from GS 4586 shows thin prisms only 0·025 mm. across in some fragments and up to 0·03 mm. in diameter in others. Prisms are 0·04 mm. in diameter in fragments from GS 4652. Prisms from the correlative Wooded Peak Limestone at Nelson, and D'Urville Island and the Waituna Stream boulder are only 0·025 mm. in diameter, but are 0·05 mm. in diameter in the Wooded Peak Limestone at Pahakorea, just south of D'Urville Island.

Variation. Most of the specimens from GS 5077 are tiny mytiliform shells, close to the holotype in shape, or narrower, with a very low *b* angle between hinge and posterior margin, and narrow *c* angle. The shells are almost smooth. A few are elongate, with a posterior wing and low wrinkles. Absence of hinge details makes identification uncertain.

Affinities. As noted by Waterhouse (1958*a*, p. 172) this species is distinguished from *A. trechmanni* (Marwick) by its wider umbonal septum. The beaks of the new species are terminal, a tiny anterior 'ear' rather than a large bulge is present in small specimens, the posterior wing is poorly developed, and the concentric wrinkles are fewer than in *A. trechmanni.*

The tiny projection of the anterior wall under the beak recalls that of *Atomodesma sp.* A, from GS 5885 of the Takitimu Group. But in the Takitimu species the projection is larger, contains the anterior part of the umbonal septum, and is not distinctly separated from the rest of the exterior by a deep depression. Also, the umbonal septum is narrower in the Takitimu form, and the beak less prosogyrous.

A. obliquatum from the Letham Formation is close in details of the umbonal region, having a similar sharp depression in front of the ligament area. But the anterior wall

next to the depression is normal to the commissure in *A. obliquatum*, and the depression is narrower. The Letham species is further distinguished from *A. woodi* by the narrower, shorter umbonal septum, the presence of a narrow posterior wing, and better developed concentric ornament. Also the ligament is constricted under the beak.

Of overseas species the closest appears to be *Aphanaia haibabensis* Reed (1935, pl. 5), a species distinguished by its strong rugae, but similar to *A. woodi* in shape and in lacking a posterior wing. *A. haibabensis* comes from the Upper Dwyka Beds of South-west Africa, considered to be Lower Permian in age (Dickins 1961*b*).

Atomodesma trechmanni (Marwick 1934)

Plate 102, figs. 2, 3, 5–7; Plate 103, figs. 1–4

Aphanaia sp. cf. *mitchelli* Trechmann 1917, p. 56, pl. 4, figs. 1–4, 8.
Maitaia trechmanni Marwick 1934, p. 948.
Maitaia trechmanni Marwick 1935, p. 295, pl. 34, figs. 1–3.
Atomodesma trechmanni Waterhouse 1958*a*, p. 171, fig. 2B.
Atomodesma (*Aphanaia*) *trechmanni* Waterhouse 1959, p. 259.

Material. The internal mould of a large right valve (holotype), and about twelve other specimens, from GS 143, preserved chiefly as natural moulds, with a wide range in size. A fine collection from this locality is kept at the British Museum (Natural History). Fragments of the hinge and more or less broken specimens come from GS 7410. Crushed specimens from GS 7411 might be conspecific. A specimen with conjoined valves from GS 7638, and other fragments. Several incomplete single valves and umbonal fragments from GS 2946. Fragments of two valves from GS 7664. A right valve and two left valves, and fragments from GS 5185.

Horizons and localities. Lower Tramway Sandstone, Permian; GS 143, 2946, 7410, ? 7411, 7638. Lower Annear Sandstone, Permian; GS ? 5185, 7664.

Holotype. TM 2033, GS 143 (Pl. 103, figs. 1, 3). *Paratypes.* TM 2304, 3678–84, 3712.

Diagnosis. Moderately high, little inflated shell, with subterminal beak, a wide anterior

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EXPLANATION OF PLATE 102

Figs. 1, 4. *Atomodesma woodi* sp. nov. 1, Internal mould TM 3637, GS 4586, showing posterior muscle scar and obscure pallial line, with ? gill suspensories nearer the beak, ×1. 4, TM 3641, GS 4652, with white and black colour bands, ×1.

Figs. 2, 3, 5–7. *Atomodesma trechmanni* (Marwick). 2, Internal mould and hinge of TM 3712, GS 143, ×1. 3, Internal mould of TM 3682 with valves conjoined but displaced, and slightly crushed, GS 143, ×2. 5, Part of internal mould TM 3684 with valves conjoined and crushed, GS 143, ×2. 6, Crushed internal mould of TM 3690, GS 2946, ×1. 7, Right valve of TM 3678, with anterior margin crushed to simulate an ear; contrast the small posterior wing and smooth shell with that in specimens from the same locality shown in figs. 2, 3, and 5; GS 143, ×1.

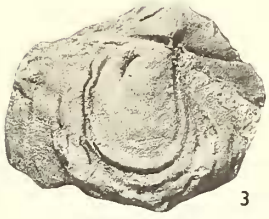
EXPLANATION OF PLATE 103

Figs. 1–4. *Atomodesma trechmanni* (Marwick). 1, 3, Mould and cast of umbonal region of holotype, TM 2033, GS 143, ×1. 2, Internal mould of TM 3705, GS 5185, ×1. 4, Rubber latex cast of umbonal region, TM 3685, GS 7410, ×2.

Figs. 5–7. *Atomodesma trabeculum* sp. nov. 5, Holotype, rubber latex cast, showing thick hinge, TM 3708, GS 7637, ×2. 6, Mould of holotype, ×1. 7, Rubber latex cast of umbonal region, showing septum unusually well developed for the species, TM 3703, GS 7637, ×2.

1

2



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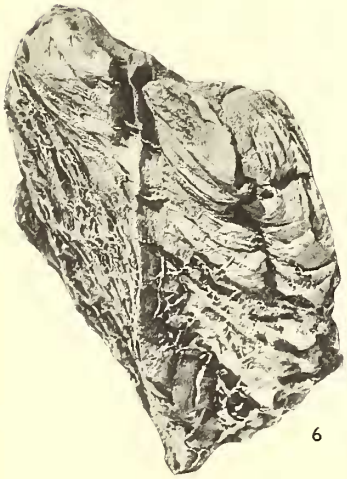

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WATERHOUSE, *Atomodesma*

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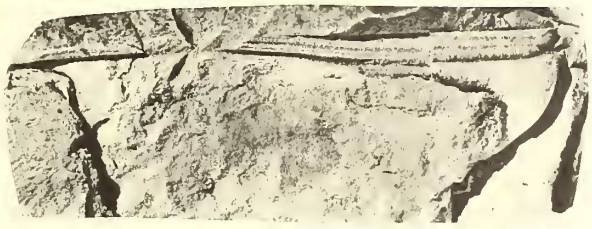
2



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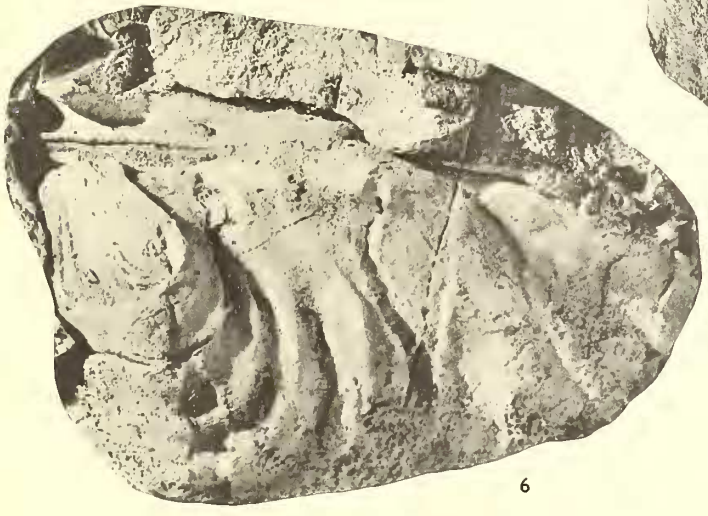

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WATERHOUSE, *Atomodesma*